

1 **Human impacts and aridity differentially alter soil N availability in drylands worldwide**

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99 **Abstract**

100 **Aim** Although very likely to co-occur in the future, it is largely unknown how simultaneous

101 increases in aridity and anthropogenic disturbances will influence the N cycle in dryland soils, the  
102 largest terrestrial biome on the planet. Climate and human impacts are changing the inputs to, and  
103 losses from, the nitrogen in terrestrial ecosystems. However, our knowledge of how the interaction  
104 between these drivers will affect the concentration of available N for plants and microorganisms as  
105 well as the dominance of N forms is still scarce and no study has yet explored these interactive  
106 effects on the N cycle at global scale.

107 **Location** 224 dryland sites from all continents except Antarctica widely differing in their  
108 environmental conditions (from arid to dry-subhumid sites) and human influence (based on distance  
109 to towns and roads and population size).

110 **Methods** Using a standardized field survey, we measured the plant cover, aridity, human impacts  
111 (i.e., proxies of land uses and air pollution), key biophysical variables (i.e., pH, texture and plant  
112 cover) as well as six N cycle important variables: total N, organic and inorganic N and N  
113 mineralization rates. We use structural equation modeling to assess the direct and indirect effects of  
114 aridity and human impacts together with key biophysical variables on the N cycle.

115 **Results** Human impacts increased the concentration of total N, while aridity decreased it. The  
116 effects of aridity and human impacts on the N cycle were spatially disconnected, which may favor  
117 N scarcity in the most arid areas and promote N accumulation in the least arid areas. Both  
118 increasing aridity and human impacts will enhance the dominance of inorganic N forms.

119 **Main Conclusions** Our findings provide evidence that human impacts will promote the  
120 accumulation of N in dryland soils worldwide, while the opposite effect is observed from increasing  
121 aridity. Interestingly, we found that these two global change drivers are spatially disconnected in  
122 drylands, favoring N losses in the most arid, and accumulation in the least arid ecosystems. Our  
123 analyses suggest that both increasing aridity and human impacts will enhance the relative  
124 dominance of inorganic N in drylands soils which may negatively impact key ecosystem functions  
125 and services at the global scale.

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127 **Keywords:** Aridity, Human impacts, Global change, N cycle, Mineralization,  
128 Depolymerization.

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134 **Introduction**

Human activities such as grazing, fertilization, intensive agriculture and fossil fuel combustion are changing the inputs to, and losses from, the nitrogen (N) cycle in terrestrial ecosystems globally (Vitousek *et al.*, 1997; Cui *et al.*, 2013). Anthropogenic N inputs have already doubled the total amount of N fixed naturally by terrestrial and aquatic ecosystems. Current annual rates of both organic and inorganic N deposition are about 124 Tg N per year (Gruber & Galloway, 2008; Schlesinger, 2009; Cornell, 2011). Human pressure on the N cycle is expected to increase during this century because of the predicted increases in global population by 36% over the next 40 years (Charles *et al.*, 2008) and the intensification of land use required to support their demand for food (OECD-FAO 2011), which is estimated to increase by 70-100% by 2050 (World Bank, 2008). For example, human impact such as N deposition derived from fossil fuel combustion and fertilizer production is increasing the availability of N (particularly in inorganic forms) in terrestrial ecosystems (Cui *et al.*, 2013; Gruber & Galloway, 2008; Schlesinger, 2009).

Paralleling the increase of N inputs derived from human activities is an increase in aridity, predicted to increase the total area of drylands (arid, semi-arid and dry-subhumid ecosystems) globally by 10% by the end of this century (Feng & Fu, 2013). Increasing aridity has been predicted to reduce soil N availability in drylands globally and to reduce the pools of organic N in these ecosystems (Schlesinger *et al.*, 1990; Delgado-Baquerizo *et al.*, 2013). These changes are predicted to exacerbate processes leading to land degradation and desertification in drylands, which are estimated to affect more than 250 million people, mostly living in developing countries (Reynolds *et al.*, 2007).

Human (i.e., air pollution and changes in land use) and climate change impacts are key drivers of ongoing global environmental change (Gruber & Galloway, 2008; Schlesinger, 2009; Canfield *et al.*, 2010; Liu *et al.*, 2010; Bai *et al.*, 2013), and are interrelated in complex ways. These global change drivers may act in opposition, or interact to accelerate their effects on natural communities. The combined impacts derived from human activities and climate change may create a more arid environment that is also characterized by reduced biological control of the N cycle (as explained in Schlesinger *et al.*, 1990). For instance, direct anthropogenic-driven disturbances (e.g. overgrazing) and increases in aridity may have negative impacts on plant growth in drylands (Gruber & Galloway, 2008; Delgado-Baquerizo *et al.*, 2013), thereby reducing inputs of organic N in these ecosystems. The human impacts of N cycle have been largely studied at local scale. For example, Baker *et al.*, (2001) concluded that in Phoenix, the urban and agricultural components of the ecosystem were an order of magnitude higher than inputs to the desert, increasing the amount of N in soil and groundwater pools and promoting losses to rivers. Similarly, nutrient enrichment derived from human activities has been also observed to locally enhance N mineralization in the

169 Sonora desert (Hall *et al.*, 2011). However, little is known on how the interaction between  
170 increasing aridity and human impacts will affect the concentration of available N for plants and  
171 microorganisms as well as the dominance of N forms and no study has yet explored these  
172 interactive effects on the N cycle in global drylands.

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174 Drylands form the largest terrestrial biome on Earth and support over 38% of its population  
175 (Reynolds *et al.*, 2007; Schimel, 2010). Nitrogen is, after water, the most important factor limiting  
176 net primary production and organic matter decomposition in these areas (Robertson & Groffman,  
177 2007; Schlesinger & Bernhardt, 2013). The N cycle is therefore crucial for ecosystem functioning  
178 and the provision of ecosystem services in these areas (Robertson & Groffman, 2007; Schlesinger  
179 & Bernhardt, 2013; Compton *et al.*, 2011). Knowing how direct and indirect effects from climatic  
180 (i.e., aridity), biophysical (i.e., soil texture, pH and plant cover) and anthropogenic (i.e., human-  
181 induced climate change, air pollution and land use changes) drivers jointly impact the N cycle is  
182 crucial if we are to improve our ability to predict the ecological consequences of climate change for  
183 terrestrial ecosystems (Schlesinger *et al.*, 1990, Gruber & Galloway, 2008; Chen *et al.*, 2013).

184 We conducted a global mensurative study of 224 field sites from all continents except Antarctica to  
185 evaluate how aridity and human impacts, together with biotic (plant cover) and abiotic (soil texture  
186 and pH) factors, will affect total N, dissolved organic N, ammonium and nitrate concentrations,  
187 dissolved organic-to-inorganic N (DON:DIN) ratio and the potential net mineralization rate of  
188 dryland soils. These variables were selected because they are good proxies of N availability and  
189 dominance of N forms within soils (Schimel & Bennett, 2004; Delgado-Baquerizo & Gallardo,  
190 2011). We hypothesized that: i) soil total N concentration would be enhanced by human impacts  
191 (estimated indirectly using proxies) and decline with aridity (Delgado-Baquerizo *et al.*, 2013); and  
192 ii) aridity and human impacts will negatively affect the biological control of the N cycle (e.g.,  
193 reducing plant cover), resulting in an increasing dominance of inorganic N forms and processes  
194 (i.e., mineralization) in dryland soils (Schlesinger *et al.*, 1990).

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## 196 **Material and Methods**

### 197 Study area

198 This study was restricted to dryland ecosystems, defined as regions with an aridity index (AI =  
199 precipitation/potential evapotranspiration) between 0.05 and 0.65 (UNEP 1992). Original field data  
200 were collected at 224 sites located in 16 countries from all continents except Antarctica. The sites  
201 surveyed encompass a wide variety of vegetation types typically found in drylands, including  
202 grasslands, shrublands, savannas, dry seasonal forests and open woodlands dominated by trees.

203 Mean annual precipitation and temperature of the study sites ranged from 66 to 1219 mm and from  
204 -1.8 to 27.8°C, respectively. See Maestre *et al.*, (2012) for additional details on the study sites.

205 Climatic, abiotic, plant and nitrogen variables measured

206 Data collection was carried out between February 2006 and December 2010 according to a  
207 standardized sampling protocol. The cover of vascular plants at each site was measured using four  
208 30-m transects and the line-intercept method, as described in Maestre *et al.*, (2012). The coordinates  
209 of each plot were recorded *in situ* with a portable Global Positioning System, and were standardized  
210 to the WGS84 ellipsoid for visualization and analyses. Aridity (1-aridity index) was estimated using  
211 data from the Worldclim global database (Hijmans *et al.*, 2005). Soils (0-7.5 cm depth) were  
212 sampled during the dry season under the canopy of the dominant perennial plants, and in open  
213 plant-free areas (10-15 samples were sampled per site, over 2600 samples in total). After field  
214 collection, the soil samples were taken to the laboratory, where they were sieved (2 mm mesh), air-  
215 dried for one month and stored in this condition until laboratory analyses. All the soil analyses in  
216 this study were carried out with air-dry samples for logistical reasons. Previous studies have shown  
217 that in drylands such as those we studied, air drying and further storage of soils does not  
218 appreciably alter the functions of interest in this study (Zornoza *et al.*, 2006, 2009). It is also  
219 important to note that our sampled soils were collected when the soil was in this dry state. Thus, the  
220 potential bias induced by our drying treatment is expected to be minimal.

221 Soil texture was measured in two to three composite samples per site, as preliminary analysis  
222 revealed that within-site variability was very low. One composite sample each per microsite (open  
223 areas or soil under the canopy of the dominant perennial plants) and site were analyzed for sand,  
224 clay and silt content according to Kettler *et al.*, (2001). Soil pH was measured in all the soil samples  
225 with a pH metre, in a 1: 2.5 mass: volume soil and water suspension. We also measured multiple  
226 variables from the nitrogen (N) cycle (total N, mineralization rate, dissolved inorganic N [DIN; sum  
227 of  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ] and DON) as described by Maestre *et al.*, (2012). In brief, soil samples (2.5 gr of  
228 soil) were extracted with  $\text{K}_2\text{SO}_4$  0.5 M in a ratio 1:5. Soil extracts were shaken in an orbital shaker  
229 at 200 rpm for 1 h at 20°C and filtered to pass a 0.45- $\mu\text{m}$  Millipore filter (Jones & Willett, 2006).  
230 The filtered extract was kept at 4°C until colorimetric analyses. Using the indophenol blue method  
231 (Sims *et al.*, 1995), we estimated concentrations of ammonium and nitrate (colorimetrically) and  
232 available N (after potassium persulphate digestion in an autoclave at 121°C over 55 minutes; Sollins  
233 *et al.*, 1999). DON was determined as the difference between available N and inorganic N (sum of  
234 ammonium and nitrate). The ratio DON:DIN was determined from these data. Regarding potential  
235 mineralization rate, air-dried soil samples were re-wetted to reach 80% of their water holding  
236 capacity and incubated in the laboratory for 14 days at 30° C (Allen *et al.*, 1986). The potential net

237 N mineralization rate was estimated as the difference between initial and final inorganic N by  
238 following Delgado-Baquerizo & Gallardo (2011). Total N was obtained using a CN analyzer (Leco  
239 CHN628 Series, LECO Corporation, St Joseph, MI, USA). The N variables used here were selected  
240 because they are good proxies of N availability and dominance of N forms within soils (Schimel &  
241 Bennett 2004; Delgado-Baquerizo & Gallardo, 2011). All of these variables were then averaged to  
242 obtain site-level estimates by using the mean values observed in bare ground and vegetated areas,  
243 weighted by their respective cover at each site.

#### 244 Assessing human impacts

245 Quantitative estimates of the magnitude of human impacts in natural ecosystems at global scales are  
246 difficult to obtain due to the lack of available data and the wide range of processes affected by  
247 human activities (e.g., N deposition, grazing, soil erosion), their different spatial scales, and the  
248 interactions among them (Beelen *et al.*, 2013). We therefore estimated such impacts indirectly by  
249 measuring four variables at each study site: average proximity (in km) to the nearest northern,  
250 southern, eastern and western paved roads from each plot, average proximity (in km) to the four  
251 nearest towns/cities from each plot, average population of the four nearest towns/cities to each plot  
252 in the last census available (number of people; Table S1), and population density of the province or  
253 region of each plot in the most recent available census (number of people·km<sup>-2</sup>; Table S1). Due to  
254 the large distances between some of our study sites and the nearest towns/cities, we considered the  
255 four closest cities to our plots, as an average value of the local human impact. Distances to nearest  
256 roads, urban centres and human population are classic proxies of human perturbation on ecosystem  
257 health and services (Schlesinger & Harley, 1992; Gill *et al.*, 1996; Drechsel *et al.*, 2001; Liu *et al.*,  
258 2010; Beelen *et al.*, 2013). We assumed that the size of the negative effects of humans on the N  
259 cycle, such N deposition and/or soil erosion, would be directly related to the distance of each site to  
260 the nearest city/town and paved road, or in densely populated areas (Drechsel *et al.*, 2001; Gadsdon  
261 & Power, 2009; Gilbert *et al.*, 2009; Liu *et al.*, 2010; Beelen *et al.*, 2013). Similarly, soil N  
262 depletion derived from land use changes have been observed to be linked to increasing local human  
263 population size (Drechsel *et al.*, 2001; Canfield *et al.*, 2010).

264 As the four surrogates of human impacts considered were highly correlated, we conducted a  
265 principal component analysis (PCA) to reduce them to independent components. Before conducting  
266 the PCA, all the human impact proxies were log-transformed to normalize them. We retained the  
267 two first components from the PCA for further analyses. These had an eigenvalue higher than 1, and  
268 together explained 80.5% of the variance in the PCA. The first component of the PCA (HC1) was  
269 highly related to the average distance to the four nearest towns/cities from each plot (Pearson's  $r =$   
270 0.96), average distance to the nearest northern, southern, eastern and western paved roads from each



plot (Pearson's  $r = 0.76$ ) and population density of the province of each plot in the most recent available census (Pearson's  $r = 0.71$ ). The HC1 was positively related to other indexes of human influence (Fig. S1a) and footprint (Fig. S1b). In addition, our HC1 was positively related to estimates of inorganic N deposition (Fig. S2a), and fertilizer application (Fig. S2b), and to the amount of N in livestock manure production (Fig. S2c). Similarly, our HC1 was positively related to the percentage land areas used as cropland (Fig. S3a) and to estimates of soil degradation (Fig. S4a). The second component of the PCA (HC2) was highly related to the average population size of the four nearest towns/cities during the most recent census (Pearson's  $r = 0.90$ ). This component was positively related to the previous human influence and footprint indexes (Fig. S1b). In addition, our HC2 was positively related to estimates of N in manure production (Fig. S2c), soil degradation (Fig. S4a) and infiltration of water, determined at our study sites (Fig. S4b). We acknowledge that variables such as fire frequency (Durán *et al.*, 2009), N deposition (Ochoa-Hueso *et al.*, 2011) and/or grazing intensity (Qiu *et al.*, 2013) at each study site would have provided better estimates of human impacts on the N cycle. However, these data were not available for most countries, as the available historical archives do not have the resolution required to obtain such data at the spatial scale of the sampled plots. Geographic distances were obtained with Google Earth® ([www.google.com/earth/index.html](http://www.google.com/earth/index.html)), while population data were gathered from official statistics of each country (see Table S1).

#### 289 Statistical analyses

We used structural equation modeling (SEM) to determine the relative importance of human impacts (HC1 and HC2), aridity, pH, sand content, plant cover and the spatial influence (distance from equator and longitude) on the different N variables evaluated. We first established an *a priori* model (Fig. S5), based on the known effects and relationships among the drivers of the N cycle (Supplementary Methods S1). Total N, concentrations of ammonium, nitrate and DON, DON:DIN ratios, and pH were log-transformed to improve linearity in the relationships between the variables in our SEM models. Similarly, plant total cover and sand content were square root transformed. We found that all N metrics, sand content and HC1 showed unimodal relationships with aridity. To introduce these second-order polynomial relationships into our SEM model, we calculated the square of aridity and introduced it into our model using a composite variable (Fig. S5). Similarly, the human impact and spatial influence metrics were also included as composite variables. The use of composite variables does not alter the underlying SEM model, but collapses the effects of multiple conceptually-related variables into a single composite effect, aiding interpretation of model results (Grace, 2006). We also examined the distributions of all of our endogenous variables (those with arrows pointing to them within the *a priori* model structure), and tested their normality.

305 Because some of the variables introduced were not normally distributed, the probability that a path  
306 coefficient differs from zero was tested using bootstrap tests (Schermelleh-Engel *et al.*, 2003). Our  
307 *a priori* model structure satisfactorily fitted to our data, as suggested by non-significant  $\chi^2$  values ( $\chi^2$   
308 = 4.740;  $P = 0.315$ ;  $d.o.f = 4$  in all cases), non-parametric Bootstrap  $P = 0.302$  and by values of  
309 RMSEA = 0.029 with a  $P = 0.569$ .

310 To aid final interpretation in light of this ability of SEM, we calculated the standardized total  
311 effects (direct plus indirect effects from the structural equation model) of human impacts (HC1 and  
312 HC2), aridity, pH, sand content, plant cover and spatial influence (longitude and distance from  
313 equator) on the selected N metrics (Grace, 2006). The net influence that one variable had upon  
314 another was calculated by summing all direct and indirect pathways between two variables. All the  
315 SEM analyses were conducted using the software AMOS 20 (IBM SPSS Inc, Chicago, IL, USA).

316 Finally, we explored the relationship between the different N variables and human impacts  
317 (HC1 and HC2) within each of the studied dryland ecosystems: arid, semiarid and dry-subhumid.  
318 By doing this, we wanted to check what dryland ecosystems suffer the highest impact on N cycle  
319 derived from human activities. Because our data were not normal, we determined our cross-validate  
320  $R^2$  (CV  $R^2$ ; percent of squared error explained by the model compared to the null model) and  $P$ -  
321 values using the A3 package from R (Fortmann-Roe *et al.* 2013).

322

## 323 Results

324 Sand content, pH and total plant cover in our study ranged from 5.36 to 97.94%, 4.13 to 9.21 and  
325 2.83 to 82.88% respectively (Table S2). Similarly, for the studied N variables, total N ranged from  
326 0.01 to 0.45%, ammonium from 0.82 to 55.86 mg N kg<sup>-1</sup> soil, nitrate from 0.00 to 92.07 mg N kg<sup>-1</sup>  
327 soil, DON from 1.24 to 43.31mg N kg<sup>-1</sup> soil and potential mineralization rate from -2.13 to 5.01 mg  
328 N kg<sup>-1</sup> soil day<sup>-1</sup> (Table S2).

329 Aridity was directly and negatively related to soil total N whereas human impacts (HC1 and  
330 HC2) were directly positively related to the latter (Fig. 1a). Interestingly, HC1 was negatively  
331 related to aridity (Fig 1; Fig. 2), however, aridity and HC2 were unrelated (Fig. 2). Aridity and  
332 human impacts, together with sand content, were the most important factors controlling soil total N  
333 as shown by the size of their total effects (Fig. 3a). Moreover, the total (direct plus indirect) effect  
334 of distance to towns and roads (HC1) and population size (HC2) showed opposite effects on soil  
335 total N (Fig. 3a). In absolute terms, however, the impact of HC1 was higher than that of HC2,  
336 resulting in a net total positive effect of human impacts on this variable (Fig. 3a).

337 Increases in both aridity and human impacts were associated to decreases in the DON:DIN  
338 ratio (Figs. 1b, 2b), and increases on potential net mineralization rates (Figs. 1c, 2c). Our different

339 surrogates of anthropogenic disturbances (HC1 and HC2) rendered different and opposite  
340 relationships with DON and soil nitrate, although both were associated to increasing ammonium  
341 concentrations (Fig. 3e). HC1 showed a positive relationship with the concentrations of DON and  
342 soil nitrate whereas HC2 was negatively associated with those N variables.

343 Dry-submid were the dryland ecosystem with the highest positive and negative relationship  
344 between HC1 and total N and HC1 and DON:DIN ratio, respectively (Fig. 4). However, the  
345 opposite effect was observed from HC1 on total N in dry-subhumid ecosystems (Fig. S6). In  
346 addition, the dry-submid ecosystems showed the highest positive relationship between HC1 and  
347 potential mineralization and nitrate concentration (Fig. 4). Again, the opposite effect was observed  
348 from HC2 on nitrate and mineralization for dry-subhumid ecosystems (Fig. S6).

349

## 350 **Discussion**

### 351 *Global change impacts on soil total N*

352 Although human activity should increase the N budget worldwide (Galloway *et al.*, 2008), our  
353 results suggest that the increases in aridity forecasted for large areas of the planet will counteract  
354 such increment in total N. Of particular interest was the observed negative relationship between  
355 aridity and human impacts in our models. This is likely derived from the constraints that aridity, and  
356 hence shortage in water availability, generally impose on human activities and urban development  
357 (Whitford, 2002; Schwinning & Sala, 2004). In particular, we found a quadratic negative  
358 relationship between aridity and HC1. This result suggests that there is a current spatial disconnect  
359 between the impacts of aridity, which may favour N losses, and those of human activities, which  
360 may favor N accumulation, in different dryland regions (Liu *et al.*, 2012). Thus, at the global scale,  
361 the driest regions will tend to become more N limited, but N enhancement due to human activities  
362 in the least arid drylands may counteract any trend towards greater N limitation. In addition, aridity  
363 and HC2 were unrelated, suggesting that increasing aridity is related to more scattered urban areas  
364 (HC1), but do not population density in general (HC2; Mainguet, 1999). We stress that the spatial  
365 distribution of our plots did not cover areas where this pattern may not hold, such as large, rapidly -  
366 growing desert urban areas (e.g. Phoenix or Las Vegas in USA; Kane 2014) or semi-arid areas with  
367 intensive agricultural activities (e.g. Almería in SE Spain; Aznar-Sánchez & Galdeano-Gómez,  
368 2011). We also would like to acknowledge the limitations of the observational approach followed,  
369 however we believe that our study provide a good snapshot of the status of N cycle at a global scale,  
370 and show from an integrative point of view how interactive effects derived from aridity and human  
371 impacts can globally affect N concentrations and dominance of relative N forms.

372

373 *Inorganic N accumulation derived from global change*

374 Increasing human impacts and aridity resulted in direct and total negative impacts on the DON:DIN  
375 ratio, and a positive direct effect on potential net mineralization rates. Thus, any increase in human  
376 impacts and aridity derived from global change will lead to a greater dominance of inorganic N  
377 forms. This scenario is compatible with both the observed loss of biological control on N cycle  
378 derived from climate change suggested by Schlesinger *et al.*, (1990) and Delgado-Baquerizo *et al.*,  
379 (2013), and the trend to an inorganic N saturation stage predicted by models in terrestrial  
380 ecosystems as a consequence of anthropogenic N deposition (Fig. S2a; Gruber & Galloway 2008;  
381 Schlesinger, 2009; Chen *et al.*, 2013). An increase in aridity has been suggested to result in a world  
382 with a lower net depolymerization rate (DON production) in the most arid areas, likely linked to the  
383 low precipitation and plant cover of these environments (Schlesinger *et al.*, 1990), which would  
384 increase the dominance of inorganic N forms. This was supported by the direct negative relationship  
385 between aridity and DON:DIN found. However, this direct negative effect was counteracted by the  
386 indirect positive effects mediated through sand content and pH, both increasing the ratio DON:DIN  
387 (Fig. 1b). As a consequence of the interplay between direct negative and indirect positive effects,  
388 the total effect of aridity on the dominance of dissolved organic versus inorganic N forms was  
389 negligible (Fig. 2b). Conversely, proximity to human populations (HC1) was the most important  
390 factor controlling the DON:DIN ratio as shown by its total effect size, which was greater than for  
391 any other factors evaluated (Fig. 2b). This decrease in the DON:DIN ratio with increasing human  
392 impact may be driven by the increase of inorganic N inputs linked to human activities such as  
393 fertilizer production, accumulation of livestock wastes and fossil fuel combustion in the vicinity of  
394 our sites (Dentener *et al.*, 2006; Cornell, 2011). An increase in inorganic N in soils may have a  
395 negative impact on the functioning and services provided by drylands worldwide. For example,  
396 Delgado-Baquerizo *et al.*, (2013b) found that inorganic N inputs were negatively linked to  
397 microbial functional diversity and N depolymerization (production of DON), and may also reduce  
398 the organic N uptake by plants and microorganisms in these ecosystems (Warren, 2009).

399 *Shifts in the different N forms derived from human impacts*

400 The relatively strong total positive relationship between HC1 and DON concentrations may suggest  
401 that atmospheric deposition of organic N, which has rarely been considered a significant source of  
402 atmospheric N (Cornell *et al.*, 2011), may be affecting DON concentration in dryland soils. In  
403 addition, HC1 was positively related to the concentrations of soil nitrate and ammonium, suggesting  
404 the importance of both reduced and oxidized N deposition in global drylands. Because our sites are  
405 not located in agricultural areas, the effect of highly populated towns surrounding our plots (HC2)  
406 should be related more to the use of these drylands for grazing and wood harvesting than to more

intensive human uses. Overgrazing can lead to losses of soil organic matter and nutrients through the conversion of semiarid grasslands to arid shrublands (Schlesinger *et al.*, 1990). However, HC2 was positively related to N in manure production at the global scale (Fig. S2c). This constitutes one of the most important sources of reduced N to the atmosphere (Bouwman *et al.*, 2011), and may explain why the observed negative effect of HC2 on DON and nitrate by intensive agriculture is not found with ammonium. Intensive land management may result in DON and nitrate leaching into streams and the groundwater, which may pollute them (Gruber & Galloway 2008; Schlesinger 2009; Chen *et al.*, 2013). However, both HC1 and HC2 were positively related to the concentration of ammonium in soil (Fig. 2e). Ammonium is one of the most common N sources associated with human activities, as intensive agriculture and livestock are significant sources (Anderson *et al.*, 2003; Clarisse *et al.*, 2009; Canfield *et al.*, 2010). Increases in the concentration of soil ammonium with increasing human impacts in this study suggest that at least a part of the ammonium present in dryland soils may come from human-derived activities. Overall, this increase in soil ammonium concentrations may increase the potential of N to cross ecosystem boundaries by ammonia volatilization or through ammonium conversion to nitrate followed by leaching from soil, all of which are common phenomena in drylands and may cause eutrophication and reduce water quality (Schlesinger *et al.*, 1990; Schlesinger & Harley, 1992; Robertson & Groffman, 2007; Ravishankara *et al.*, 2009). For example, as processes such as nitrification usually require small amounts of water (Schwinning & Sala 2004; Delgado-Baquerizo *et al.*, 2013c), the accumulation of ammonium in the less arid drylands may quickly promote its conversion to nitrate after even small rainfall events (Schwinning & Sala, 2004). Our study supports this, as we observed an increase in the potential net nitrification rate in our soils with increasing ammonium ( $P < 0.001$ ; Fig. S7). The overall dominance of inorganic forms of N resulting from increasing aridity and human impacts may enhance nitrification and denitrification rates in drylands, (e.g. releasing  $N_2O$ ; Schlesinger *et al.*, 2009; Canfield *et al.*, 2010), potentially enhancing the emission of greenhouse gases from these ecosystems.

433

## 434 **Conclusions**

Our findings provide evidence that human impacts promote the accumulation of N in dryland soils worldwide, but that these effects are offset by increases in aridity. We also found that these two global change drivers are spatially disconnected in drylands, favoring N losses in the most arid, and accumulation in the least arid ecosystems. Our analyses indicate that both increasing aridity and human impacts linked to the intensity of anthropogenic disturbance will enhance the inorganic control of the N cycle in drylands soils. This increase in inorganic N dominance in dryland soils

may have negative effects on key ecosystem functions (e.g. microbial functionality) and services (e.g. quality of water and air) at the global scale, and may enhance the emission of important greenhouse gases such as N<sub>2</sub>O.

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## References

- Allen SE, Grimshaw HM, Rowland AP (1986) *Chemical analysis. Methods in plant ecology*. Blackwell Scientific, Oxford, UK.
- Anderson N, Strader R, Davidson C (2003) Airborne reduced nitrogen ammonia emissions from agriculture and other sources. *Environment International*, **29**, 277-289.
- Aznar-Sánchez JA, Galdeano-Gómez E (2011) Territory, Cluster and Competitiveness of the Intensive Horticulture in Almería, Spain. *Open Geography Journal*, **4**, 103-114.
- Bai E *et al.* (2013) A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist*, **199**, 441-451.
- Beelen R *et al.* (2013) Development of NO<sub>2</sub> and NO<sub>x</sub> land use regression models for estimating air pollution exposure in 36 study areas in Europe - The ESCAPE project. *Atmospheric Environment*, **72**, 10-23.
- Bouwman L *et al.* (2011) Exploring global changes in nitrogen and phosphorus cycles in agriculture induced by livestock production over the 1900–2050 period. *Proceedings of the National Academy of Sciences USA* 10.1073/pnas., 1012878108.
- Canfield DE, Glazer AN, Falkowski PG (2010) The evolution and future of Earth's nitrogen cycle. *Science*, **330**, 192–196.
- Charles H *et al.* (2010) Food Security, The Challenge of Feeding 9 Billion People. *Science*, **327**, 812-818.
- Chen H *et al.* (2013) The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biology*, **19**, 2940–2955.
- Clarisse L, Clerbaux C, Dentener F, Hurtmans D, Coheur, P-F (2009) Global ammonia distribution derived from infrared satellite observations. *Nature Geoscience*, **2**, 479-483.

475 Compton JE *et al.* (2011) Ecosystem services altered by human changes in the nitrogen cycle, a  
 476 new perspective for US decision making. *Ecology Letters*, **14**, 804-15.  
 477 Cornell SE (2011) Atmospheric nitrogen deposition, Revisiting the question of the importance of  
 478 the organic component. *Environmental Pollution*, **159**, 2214-2222.  
 479 Cui S *et al.* (2013) Centennial-scale analysis of the creation and fate of reactive nitrogen in China  
 480 1910-2010. *Proceedings of the National Academy of Sciences USA* doi,  
 481 10.1073/pnas.1221638110.  
 482 Delgado-Baquerizo M, Gallardo A (2011) Depolymerization and mineralization rates at 12  
 483 Mediterranean sites with varying soil N availability A test for the Schimel Bennett model.  
 484 *Soil Biology and Biochemistry*, **43**, 693–696.  
 485 Delgado-Baquerizo M *et al.* (2013a) Decoupling of nutrient cycles as a function of aridity in  
 486 global dryland soils. *Nature*, **502**, 672–676.  
 487 Delgado-Baquerizo M *et al.* (2013b) Biocrusts control the nitrogen dynamics and microbial  
 488 functional diversity of semi-arid soils in response to nutrient additions. *Plant Soil*, **372**, 643-  
 489 654.  
 490 Delgado-Baquerizo M *et al.* (2013c) Biological soil crusts promote N accumulation in response  
 491 to dew events in dryland soils. *Soil Biology and Biochemistry*, **62**, 22-27.  
 492 Dentener F *et al.* (2006) Nitrogen and sulfur deposition on regional and global scales, A  
 493 multimodel evaluation. *Global Biogeochemical Cycles*, **20**, doi,10.1029/2005GB002672.  
 494 Drechsel P *et al.* (2001) Population density, soil nutrient depletion, and economic growth in sub-  
 495 Saharan Africa. *Ecological Economics*, **38**, 251–258.  
 496 Durán JA *et al.* (2009) Changes in net N mineralization rates and soil N and P pools in a pine  
 497 forest wildfire chronosequence. *Biology and Fertility Soils*, **45**, 781-788.  
 498 Gadsdon SR, Power SA. (2009) Quantifying local traffic contributions to NO<sub>2</sub> and NH<sub>3</sub>  
 499 concentrations in natural habitats. *Environmental Pollution*, **157**, 2845–2852.  
 500 Galloway JN *et al.* (2008) Trends, Questions, and Potential Solutions Transformation. *Science*,  
 501 **320**, 889-892.  
 502 Gilbert NL *et al.* (2007) The influence of highway traffic on ambient nitrogen dioxide  
 503 concentrations beyond the immediate vicinity of highways. *Atmospheric Environment*, **41**,  
 504 2670–2673.  
 505 Gill JA, Sutherland WJ, Watkinson AR (1996) A method to quantify the effects of human  
 506 disturbance on animal populations. *Journal of Applied Ecology*, **33**, 786-792.  
 507 Gruber N, Galloway JN. (2008) An Earth-system perspective of the global nitrogen cycle. *Nature*,  
 508 **451**, 293–296.

509 Feng S, Fu Q (2013) Expansion of global drylands under a warming climate. *Atmospheric*  
510 *Chemistry and Physics*, **13**, 10081-10094.

511 Finzi AC *et al.* (2011) Coupled biochemical cycles, Responses and feedbacks of coupled  
512 biogeochemical cycles to climate change, examples from terrestrial ecosystems. *Frontiers in*  
513 *Ecology and Environment*, **9**, 61–67.

514 Grace JB (2006) *Structural Equation Modeling*. Natural Systems Cambridge University Press,  
515 New York, USA.

516 Hijmans RJ *et al.* (2005) Very high resolution interpolated climate surfaces for global land areas.  
517 *International Journal of Climatology*, **25**, 1965-1978.

518 Jones DL, Willett VB (2006) Experimental evaluation of methods to quantify dissolved organic  
519 nitrogen DON and dissolved organic carbon DOC in soil. *Soil Biology and Biochemistry*, **38**,  
520 991-999.

521 Kane K *et al.* 2014) A spatio-temporal view of historical growth in downtown Phoenix, Arizona.  
522 *Landscape and Urban Planning*, **121**, 70-80.

523 Kettler TA, Doran JW, Gilbert TL (2001) Simplified method for soil particle-size determination  
524 to accompany soil-quality analyses. *Soil Science Society of America Journal*, **65**, 849

525 Liu J *et al.* (2010) A high-resolution assessment on global nitrogen flows in cropland. *Proceedings*  
526 *of the National Academy of Sciences USA*, **107**, 8035–8040.

527 Maestre FT *et al.* 2012) Plant species richness ecosystem multifunctionality in global drylands.  
528 *Science*, **335**, 214-218.

529 Mainguet M (1999) *Aridity, Droughts and Human Development* Springer, NY, USA.

530 OECD/FAO 2011. OECD-FAO Agricultural Outlook 2011-2020, OECD Publishing and  
531 FAO. [http://dx.doi.org/10.1787/agr\\_outlook-2011-en](http://dx.doi.org/10.1787/agr_outlook-2011-en).

532 Peñuelas J *et al.* (2012) The human-induced imbalance between C, N and P in Earth's life  
533 system. *Global Change Biology*, **18**, 3–6.

534 Qiu L *et al.* (2013) Ecosystem Carbon and Nitrogen Accumulation after Grazing Exclusion in  
535 Semiarid Grassland. *PLoS ONE*, **8**, e55433. doi,10.1371/journal.pone.0055433.

536 Ravishankara AR, Daniel JS, Portmann RW (2009) Nitrous oxide N<sub>2</sub>O, The dominant  
537 ozone-depleting substance emitted in the 21st century. *Science*, **326**,123–125.

538 Reynolds JF. *et al.* (2007) Global desertification, Building a science for dryland development.  
539 *Science*, **316**, 847–851.

540 Robertson, G.P., Groffman, P (2007) *Soil Microbiology, Biochemistry, and Ecology*. Springer,  
541 New York, New York, USA.



542 Schermelleh-Engel K, Moosbrugger KH, Müller H (2003) Evaluating the fit of structural  
 543 equation models, tests of significance descriptive goodness-of-fit measures. *Methods of*  
 544 *Psychological Research Online*, **8**, 23-74.  
 545 Schimel JP, Bennett J (2004) Nitrogen mineralization, challenges of a changing paradigm.  
 546 *Ecology*, **85**, 591-602.  
 547 Schimel DS. (2010) Drylands in the earth system. *Science*, **327**, 418-419.  
 548 Schlesinger W.H *et al.* (1990) Biological Feedbacks in Global Desertification. *Science*, 247,  
 549 1043-1048.  
 550 Schlesinger WH, Harley PC (1992) A global budget for atmospheric NH<sub>3</sub>. *Biogeochemistry*,  
 551 **15**, 191-211.  
 552 Schlesinger WH (2009) On the fate of anthropogenic nitrogen. *Proc. Natl. Acad. Sci. USA*, **106**,  
 553 203–208.  
 554 Schlesinger WH, Bernhardt ES (2013) *Biogeochemistry, an analysis of global change*.  
 555 Academic Press, CA, USA.  
 556 Schwinning S, Sala OE (2004) Hierarchy of responses to resource pulses in arid and semi-arid  
 557 ecosystems. *Oecologia*, **141**, 211–20.  
 558 Sims GK, Ellsworth TR, Mulvaney RL (1995) Microscale determination of inorganic nitrogen in  
 559 water and soil extracts. *Communications in Soil Science and Plant Analysis*, 26, 303–316.  
 560 Sollins P, Glassman C, Paul EA, Swantston C, Lajtha K, Heil JW, Ellikott ET (1999) *Soil*  
 561 *carbon and nitrogen: Pools and fraction. Standard Soil Methods for Long-Term Ecological*  
 562 *Research*. Oxford University Press, Oxford.  
 563 UNEP 2012) *United Nations Environment Programme World Atlas of Desertification*. Edward  
 564 Arnold, London, UK.  
 565 Vitousek PM *et al.* (1997) Human alteration of the global nitrogen cycle, Sources and  
 566 consequences. *Ecological Applications*, **7**, 737–750.  
 567 Warren CR (2009) Does nitrogen concentration affect relative uptake rates of nitrate, ammonium,  
 568 and glycine?. *Journal of Plant Nutrition and Soil Science*, **172**, 224-229.  
 569 Whitford WG (2002) *Ecology of Desert Systems*. Academic Press, San Diego, CA.  
 570 World Bank (2008) *World Development Report, Agriculture for Development*. World Bank,  
 571 Washington, DC.  
 572 Zornoza R. *et al.* (2006) Assessing air-drying and rewetting pre-treatment effect on some soil  
 573 enzyme activities under Mediterranean conditions. *Soil Biology and Biochemistry*, **38**, 2125  
 574 Zornoza R. *et al.* (2009) Storage effects on biochemical properties of air-dried soil samples from  
 575 southeastern Spain. *Arid Land Restoration and Management*, **23**, 213

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## 577 **Supporting Information legends**

578 Supplementary information can be found in the online version of this article

579 **Supplementary Methods S1.** Analyzing our structural equation model: rationale for the variables  
580 included.

581 **Figure S1.** Relationships between our human impacts and previous human impact indices.

582 **Figure S2.** Relationships between our human impacts and global inorganic N deposition, N  
583 fertilizer application and the N in manure production.

584 **Figure S3.** Relationships between our human impacts and global land area used as cropland and  
585 pasture.

586 **Figure S4.** Relationships between our human impacts and the global human-induced soil  
587 degradation, and field assessed infiltration and stability.

588 **Figure S5.** A priori generic structural equation model (SEM) used in this study.

589 **Figure S6.** Relationships between aridity and our human impacts in this study.

590 **Figure S7.** Relationship between ammonium concentration and the potential net nitrification rate.

591 **Table S1.** Information about the population data used to estimate human impacts at our study sites.

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## 603 **Figure legends**

604 **Figure 1.** Effects of aridity (blue arrows), human impacts (red arrows), pH, sand content, plant  
605 cover and spatial influence (grey arrows) on: total N (a), DON:DIN ratio (b), mineralization rate (c),  
606 DON (d),  $\text{NH}_4^+$  (e) and  $\text{NO}_3^-$  (f). Numbers adjacent to arrows indicative of the effect size of the  
607 relationship. Continuous and dashed arrows indicate positive and negative relationships,  
608 respectively.  $R^2$  denotes the proportion of variance explained. For graphical simplicity, factors  
609 influencing human impacts are: a. Spatial  $\rightarrow$  HC1 = 0.13, Spatial  $\rightarrow$  HC2 = -0.35\*\*\*; b. Sand  $\rightarrow$

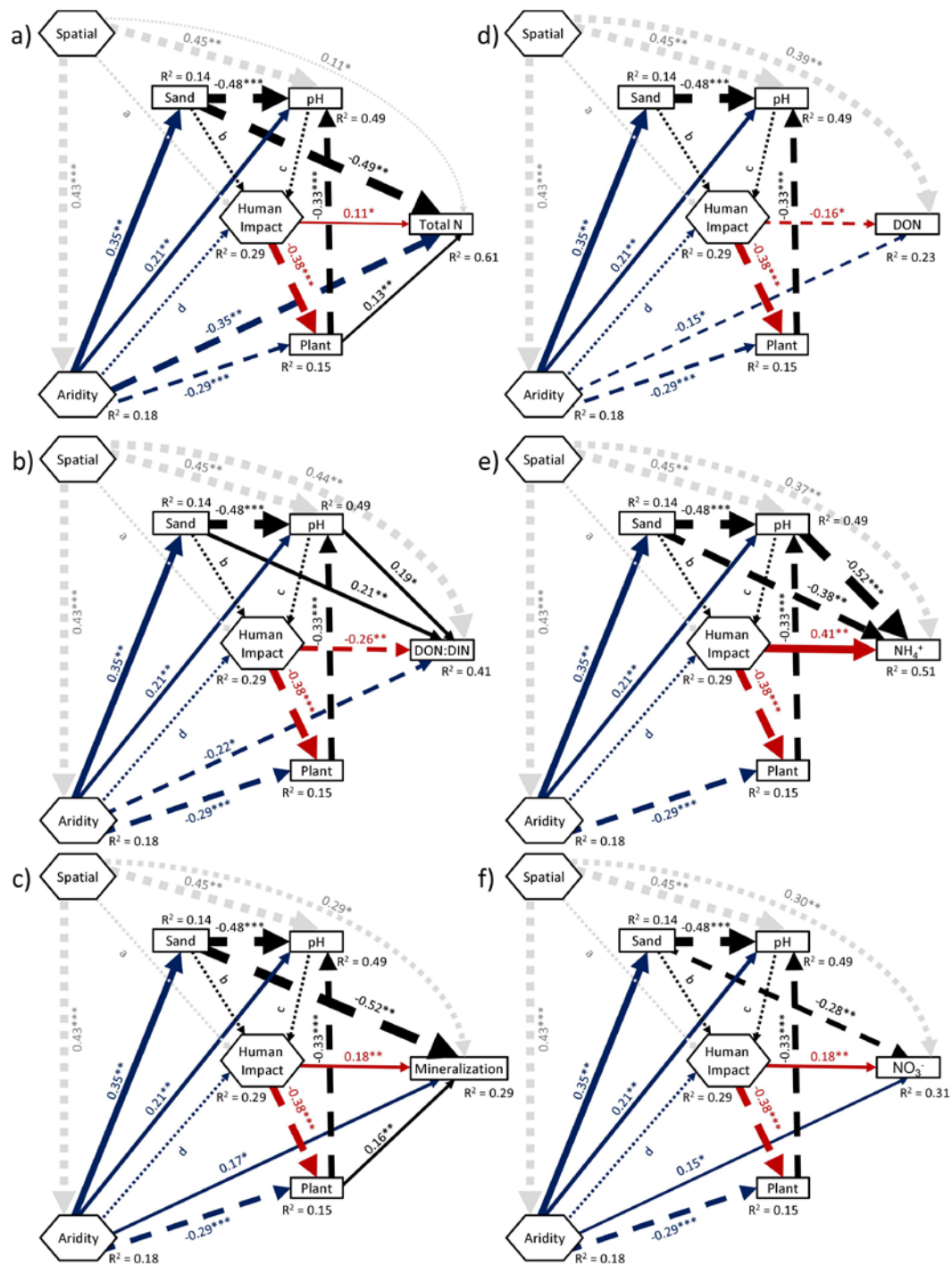
610 HC1 = -0.05, Sand  $\rightarrow$  HC2 = -0.16\*\*; c. pH  $\rightarrow$  HC1 = 0.34, pH  $\rightarrow$  HC2 = -0.37\*\*; d. Composite  
611 aridity  $\rightarrow$  HC1 = -0.43\*\*\*, Aridity  $\rightarrow$  HC2 = 0.28\*\*. Significance levels are as follows: \* $P < 0.05$ ,  
612 \*\*  $P < 0.01$  and \*\*\*  $P < 0.001$ .

613 **Figure 2.** Relationships between aridity (1- aridity index) and the first (a; HC1) and second (b;  
614 HC2) components of a principal component analysis from four proxies of human impacts:  
615 proximity to urban areas, paved roads, population density and population size. The fitted lines  
616 correspond to quadratic (a) and (b) linear models. Because our data were not normal, we determined  
617 our cross-validate R2 (CV R2; percent of squared error explained by the model compared to the null  
618 model) and P-values using the A3 package from R (Fortmann-Roe et al. 2013).

619 **Figure 3.** Standardized total effects (direct plus indirect effects) derived from the structural equation  
620 modeling, including the effects of aridity (Aridity), percentage of sand (sand), pH, plant cover  
621 (Plant), distance from equator (DE) and longitude (LON) and human impact (HC1 and HC2) on the  
622 total N (a), DON:DIN ratio (b), potential mineralization rate (c), DON (d) NH4+ (e) and NO3- (f).

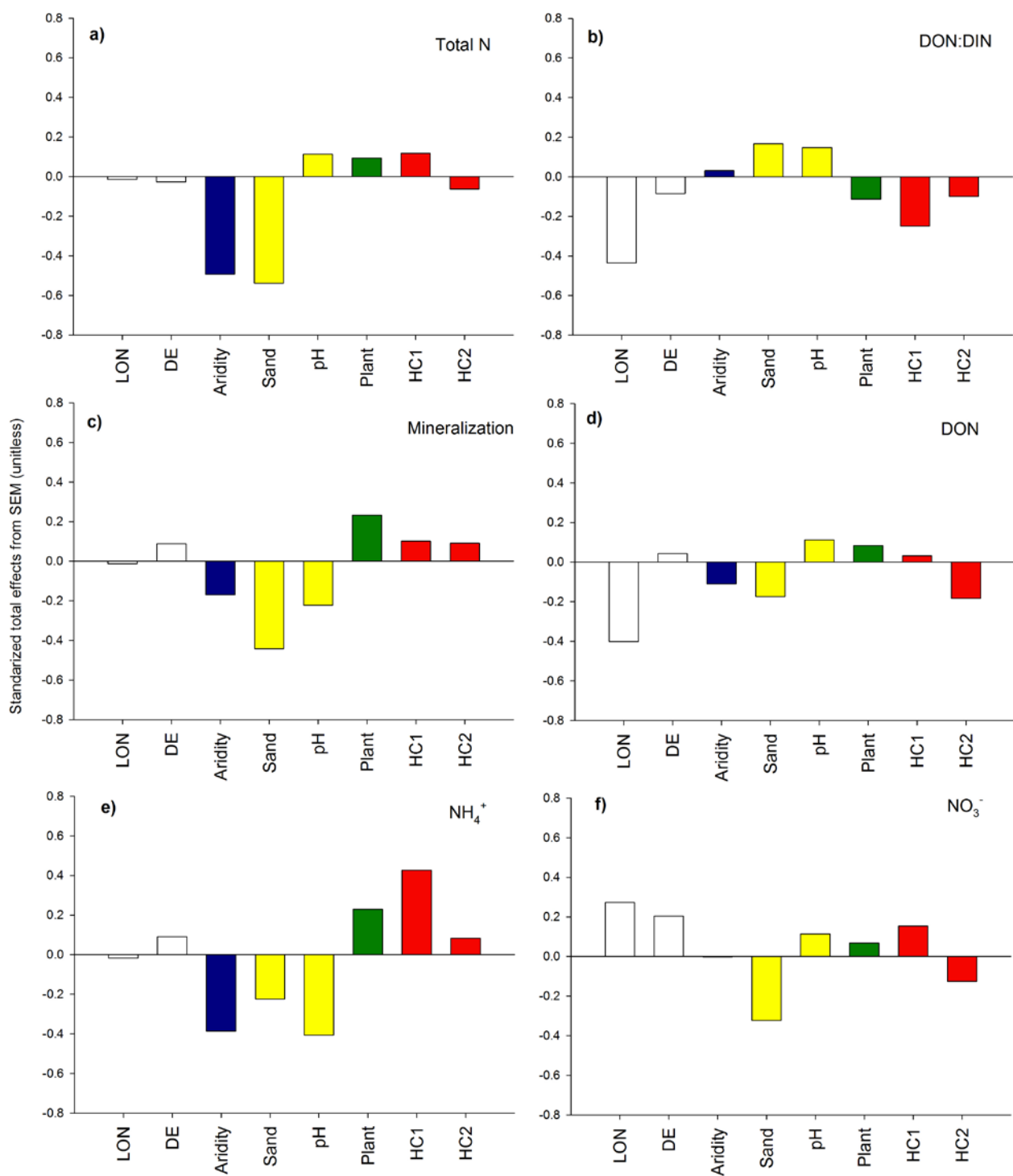
623 **Figure 4.** Relationships between the HC1 component and the different N variables: total N (a),  
624 DON:DIN ratio (b), potential net mineralization (c), DON (d), ammonium (e) and nitrate (f) for  
625 each of the studied dryland ecosystems: arid (n = 53), semiarid (n = 142) and dry-subhumid (n =  
626 29).

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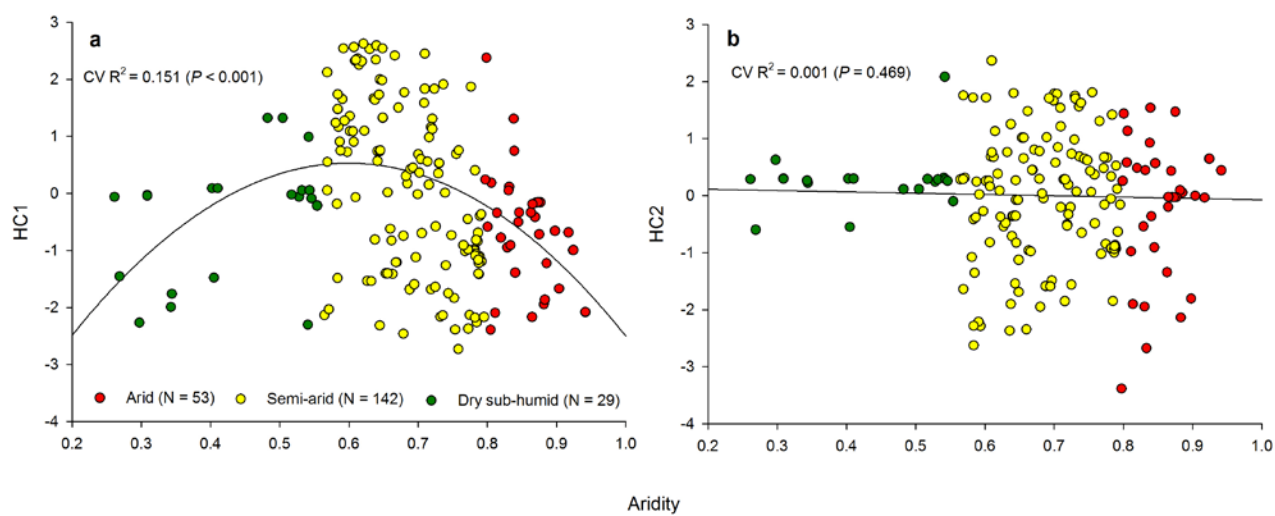


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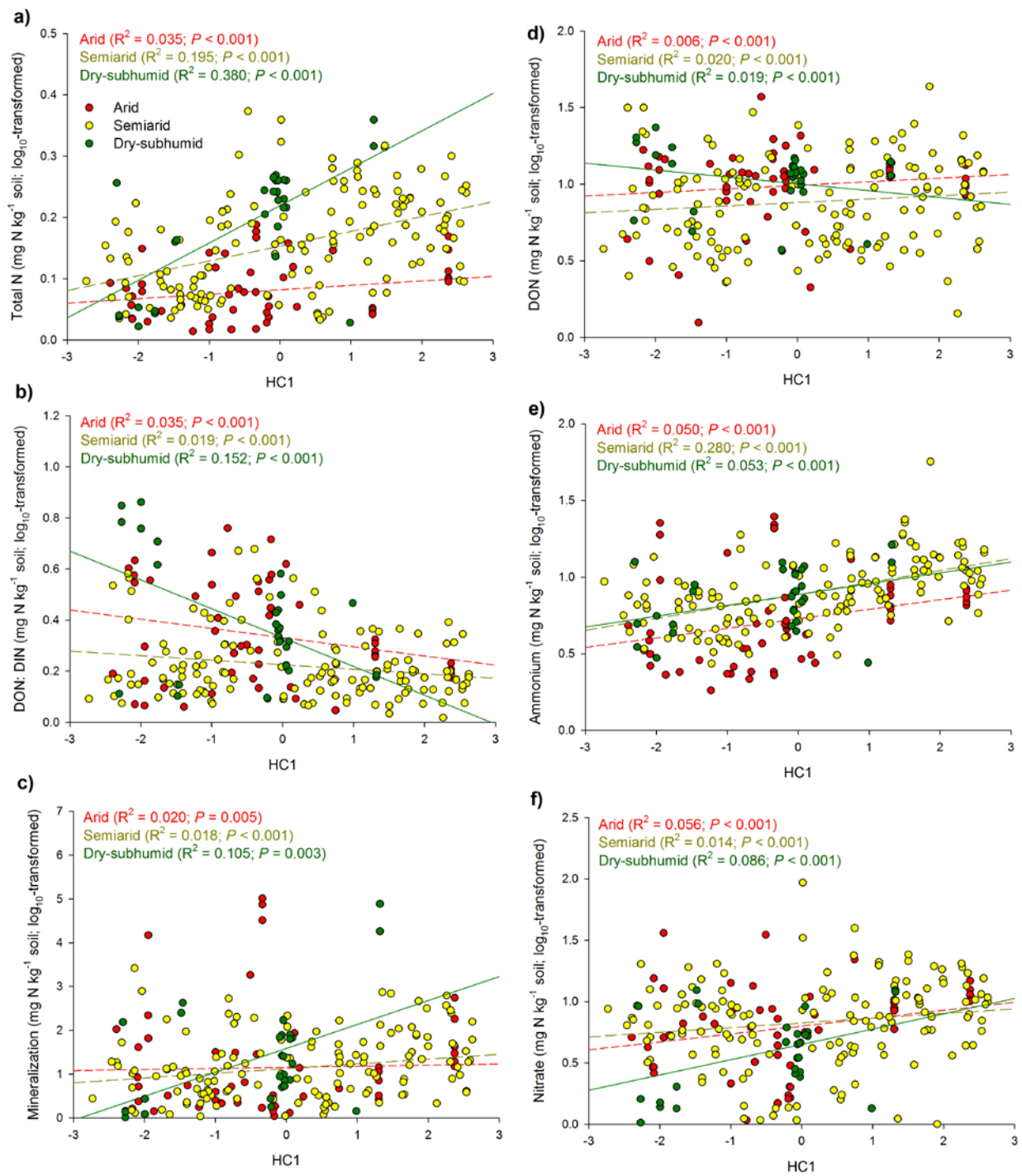
629 **Figure 1**



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631 **Figure 2**



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633 **Figure 3**



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 635 **Figure 4**  
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